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United States
Department of
Agriculture

Forest Service

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Population Ecology, Habitat Requirements, and Conservation of Neotropical Migratory Birds

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This literature review was originally prepared in support of a draft USDA Forest Service prospectus for conserving neotropical migratory birds. The prospectus combined with the literature review was distributed to about 120 participants at a planning workshop held in Atlanta, Georgia, December 10–14, 1990. Workshop participants, too numerous to list, provided verbal comments that have been incorporated into this report. Additionally, Raymond O'Connor, Jim Sweeney, and Paul Hamel provided written reviews.

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Population Ecology, Habitat Requirements, and Conservation of Neotropical Migratory Birds

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Abstract

In 1990, the National Fish and Wildlife Foundation proposed a major initiative for the conservation of migratory landbirds that breed in North America and winter in neotropical countries. This report was prepared in support of the Foundation's Neotropical Migratory Bird Conservation Program and the USDA Forest Service's role in the program. Recent analyses of local and regional bird population counts, radar migration data, and capture data from banding stations show that forest-dwelling bird species, many of which are neotropical migrants, have experienced population declines in many areas of North America. The factors that have been advanced to explain the population declines include forest fragmentation on the breeding grounds, deforestation of wintering habitats, pesticide poisoning, or the cumulative effects of habitat changes. This literature review summarizes current information on population trends of neotropical migratory birds and the factors affecting migrant populations on the breeding and wintering grounds. Opportunities for research, monitoring, and conservation of neotropical migrants on Forest Service lands are discussed.

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Population Ecology, Habitat Requirements, and Conservation of Neotropical Migratory Birds

Deborah M. Finch

OVERVIEW

GROWING CONCERNS ABOUT NEOTROPICAL MIGRANTS

Numerous studies of birds breeding in small suburban parks and woodlots of the eastern United States have shown that forest-dwelling species, a majority of which are long-distance (i.e., neotropical) migrants, experienced severe population declines between the late 1940's and the late 1980's (see review, Askins et al. 1990). Moreover, recent analyses of regional bird censuses (Robbins et al. 1989a) and migration count data (Gauthreaux, in press; Hussell et al., in press) contribute to the rising alarm that population reductions of neotropical migrants are widespread throughout North America (Terborgh 1989, Wilcove and Whitcomb 1983). Considering that neotropical migrants commonly comprise 65–85% of the breeding birds in eastern forests (Morse 1980), their drop in numbers is likely to limit opportunities for recreational bird-watching (Morton and Greenberg 1989), biological research studies, and management.

Two primary factors have been advanced to explain the population declines: forest fragmentation on the breeding grounds and deforestation of wintering habitats (Morse 1980, Terborgh 1989). If population declines are linked to specific habitat changes at local sites or physiographic regions on the breeding grounds, then migrants may be responding to land management activities in North America. Many neotropical bird species that nest away from the forest edge (so-called “forest-interior” species) disappear from forests when habitats are subdivided into smaller patches. As the proportion of edge to interior habitat expands, rates of brood parasitism and nest predation increase, inhibiting successful reproduction. Thus, in areas where large forest tracts are fragmented into small, isolated parcels by urban and resource development, impaired reproduction may disrupt the population dynamics of forest-interior species to the extent that population declines and local extinctions result.

If, on the other hand, declines in breeding bird populations are caused by deforestation or general habitat loss on the tropical wintering grounds, then population changes should be a function of migratory strategy, i.e., populations of long-distance migratory species (those migrating to the Tropics) should show changes relatively independently of short-distance migrants or residents. Analyses of Breeding Bird Survey data (a region-wide

monitoring technique) showed that 75% of forest neotropical migrant species displayed negative population trends between 1978 and 1987 (Robbins et al. 1989a), a period of accelerating deforestation rates in the Tropics. No consistent patterns of population change were detected in short-distance migrants and residents. In addition, migrants using tropical forests declined in abundance while migrants using tropical scrub habitats did not, suggesting a cause-and-effect relationship between habitat conditions on the wintering grounds and population changes in a specific group of migrants.

THE CONSERVATION CHALLENGE

Recent reviews of the literature caution readers to avoid a dichotomy in views, proposing instead that neotropical migrants are responding to the cumulative effects of multiple land use actions (Askins et al. 1990, Morton and Greenberg 1989). Although discrepancies in study results and interpretations have surfaced, the general consensus among researchers, agencies, institutions, and environmental groups is that a comprehensive and cooperative international program is needed to conserve viable populations of migrant species. In North America, data are extensive enough for managers to target individual migratory species, sets of species, and geographical areas that would benefit from conservation and management actions. Because habitat fragmentation is known to negatively affect populations of “area-sensitive” species (species that are disproportionately sensitive to declines in forest area), multiple-species management plans can be developed for groups of these species, with group composition varying by geography and habitat. Additional research is needed in many regions of North America to determine which species and habitats are vulnerable, where population declines are most severe, what factors precipitate population changes, and how viable breeding populations can be monitored and sustained.

While fewer studies have focused on bird-habitat relationships in tropical regions, several lines of evidence suggest that a wide variety of migrant species that winter in native tropical forests can survive at reduced numbers in second-growth habitats, remnant woodlots, brushy fields, and agricultural lands. Yet, preserving old-growth tropical forests in parks and reserves is likely to be the best management solution for forest species that are highly sensitive and specialized. Still, reforestation strategies and sound management of secondary habitats and rural community lands may prevent or

reduce population losses of more flexible migrant species. In this regard, the Forest Service, U.S. Department of Agriculture, can assist Latin American countries in conserving migratory landbird populations and biological diversity by supplying technical information, training opportunities, and environmental education in sustainable development, agroforestry, fuelwood management, bird and habitat monitoring, and conservation of tropical forest resources.

FURTHER READING

The following literature review provides a thorough evaluation of the factors and concepts leading up to the development of a conservation program. Research recommendations were formulated within the context of the scientific arguments and ideas evolving in the published literature. This document is intended as an information source for professionals and partners who support the conservation of neotropical migratory birds on the breeding and wintering grounds. Explicit action plans will be devised at international workshops, at national and regional meetings, by partnership working groups, and by individual agencies and organizations. For more literature on neotropical migrants or the conservation program, the following publications and reports are recommended: John Terborgh's (1989) book, *Where Have All the Birds Gone?*; the proceedings (in press) of the symposium, *Ecology and Conservation of Neotropical Migrant Landbirds*; the 1990 review article authored by Robert Askins and his colleagues in *Current Ornithology*, and the cooperative plan, *Neotropical Migratory Bird Conservation Program*, prepared by participants of a 1990 workshop in Atlanta, Georgia.

A PROGRAM TO CONSERVE NEOTROPICAL MIGRATORY BIRDS

PROGRAM DEVELOPMENT

In July 1990, the National Fish and Wildlife Foundation proposed a major initiative for the conservation of migratory landbirds that breed in North America and overwinter in the Tropics. A comprehensive program of research, monitoring, and applied management was needed to address the decline of neotropical migratory songbirds in North America. These population reductions contribute to the loss of biological diversity in the nearctic and neotropical countries where the migrants breed and winter. Most evident in forest-dwelling species, the declines have been attributed to human activities like forest fragmentation, tropical deforestation, and general habitat loss. Much alarm has been expressed about the impacts of deforestation on South American biotas, yet deforestation rates have been highest in Mexico, Central America, and the Caribbean Basin, areas where most neotropical migrants are concentrated. The Foundation proposal recommended that research and conservation efforts be focused on those countries that

supply winter habitat for the majority of neotropical migrants: Mexico, Guatemala, Belize, Honduras, Bahamas, Dominican Republic, Haiti, and Cuba.

Numerous independent activities and proposals have materialized in the last ten years to evaluate and conserve populations of neotropical migrants, but a complete, coordinated framework to ensure migrant protection was missing. The Neotropical Migratory Bird Conservation Program is designed to address this need by coordinating cooperative efforts among federal, state, and local government agencies in the United States, as well as conservation groups, professional alliances, philanthropic foundations, and private companies. Cooperation is also actively sought with government agencies, institutions, and private groups in neotropical countries and Canada. The program emphasizes that cooperative research, monitoring, and habitat management actions be implemented simultaneously in breeding and wintering areas, and that conservation activities embrace the goal of sustainable development for human populations.

PROGRAM ACCOMPLISHMENTS

To date, program accomplishments include:

- sponsorship of a planning workshop, December 10–14, 1990, in Atlanta, Georgia
- production and circulation of a report prepared by Atlanta workshop participants, entitled “Neotropical Migratory Bird Conservation Program”
- production of an interagency plan, or short version of the Atlanta report, for circulation to congressional delegates and agency representatives
- creation of a logo and motto, “Partners in Flight – Aves de las Americas”
- establishment of a Federal Interagency Committee to oversee program direction
- establishment of a Nongovernment Organization (NGO) Neotropical Migratory Bird Conservation Committee to help coordinate program direction among NGO's and other partners
- congressional appropriation of funds to support migrant conservation
- establishment of working groups to facilitate program implementation in the following topics: Research, International, Monitoring, Information and Education, and Regional (Northeast, Midwest, Southeast, West)
- signing of a programmatic Memorandum of Agreement by the following U.S. agencies and institutions: Fish and Wildlife Service, Forest Service, Bureau of Land Management, National Park Service, Agency for International Development, Environmental Protection Agency, and Department of the Navy.

ASSESSMENT OF THE NEOTROPICAL MIGRATORY BIRD SITUATION

ANALYSES OF BIRD POPULATION TRENDS

Evidence of Population Declines at Independent Sites

Spot-mapping censuses dating back to 1947 revealed that by 1978, six bird species had disappeared from Rock Creek Park, Washington, DC, and populations of several other species had declined by more than 50% (Briggs and Criswell 1978, Lynch and Whitcomb 1978, Robbins 1979). Similar long-term trends were recorded at other vicinities close to Washington, DC (Johnston and Warnings 1987, Terborgh 1989) as well as at independent sites in Georgia, New Jersey, Connecticut, Wisconsin, and New York (Ambuel and Temple 1982; Butcher et al. 1981; Leck et al. 1981; 1988; Litwin and Smith, in press; Lynch and Whitcomb 1978; Robbins 1979; Serraro 1985).

A pattern shared among these various localities was that local abundances declined primarily in forest-interior species (species whose territories are concentrated away from the forest edge, Whitcomb et al. 1981) or interior-edge species (species with territories both near the edge and in the interior of forests). Most of these were long-distance migrants (those that migrate to the Tropics) rather than short-distance migrants or residents (Askins et al. 1990). At the Washington, DC sites, long-distance migrants comprised 65–80% of the breeding birds during the 1940's and 1950's, but less than 50% at most sites by the mid-1970's (Lynch and Whitcomb 1978).

Are the Population Declines Local or Widespread?

For these local trends to represent widespread changes in eastern bird populations, the census methodology must be unbiased and comparable across years and sites; the habitats must remain constant in structure and acreage over the duration of the study; and the stands must typify those of most eastern forests (Askins et al. 1990). Though spot-mapping was the bird count method used at most sites, census results may be biased by year-to-year variability in census observers and shifts in sampling time and effort (Askins et al. 1990). In addition, habitat changes owing to forest succession (Askins and Philbrick 1987) and disturbance (Kendeigh 1982; Leck et al. 1981; Litwin and Smith, in press) probably account for population changes in some migrants. More importantly, however, the woodlands that displayed population declines were small and isolated from large forest tracts (Lynch and Whitcomb 1978, Morse 1980), suggesting the possibility that populations were exposed to a local "island effect" (*sensu* Whitcomb et al. 1976, Whitcomb 1977) rather than to broad regional or global factors. Nor can external effects be discounted because, even where study forests remained intact and undisturbed over the sampling duration, the surrounding area

typically became more developed and disrupted (Butcher et al. 1981, Robbins 1979).

Because of these complicating local effects, biologists have had difficulty linking declines of neotropical migrants to processes that may conceivably have far-reaching consequences for continental migratory populations. Though the deforestation of tropical winter habitat has been hypothesized to explain population declines of migratory birds (Morton 1980, Rappole et al. 1983, Terborgh 1989), population losses have also been ascribed to isolation and fragmentation of breeding habitat (e.g., Butcher et al. 1981, Faaborg et al. 1989, Lynch and Whigham 1984, Lynch and Whitcomb 1978, MacClintock et al. 1977). Hence, to verify the trends observed in small forest patches, Askins et al. (1990) evaluated bird censuses from four long-term population studies conducted in large, unfragmented preserves of eastern forest. If patterns of population change in extensive tracts are similar to those in isolated forest patches, the winter-habitat hypothesis would have further support.

Population Trends in Large Forest Blocks

In a 3,076-ha section of the Hubbard Brook Experimental Forest, New Hampshire, bird populations have been monitored in a 10-ha plot since 1969 (Holmes et al. 1986, Holmes and Sherry 1988). Five of 14 neotropical migrant species (Least Flycatcher, Philadelphia Vireo, Swainson's Thrush, Wood Thrush, and Blackburnian Warbler) declined significantly over this period, whereas eight migrant species exhibited no variation in abundance, and one species increased. Following a caterpillar infestation at the beginning of the study, unusually high population levels of the five bird species may have declined in response to reductions in prey densities. Forest maturation may also partially account for populations reductions in two species (Least Flycatcher and Philadelphia Vireo) associated with mid-successional stages. Thus, global declines in neotropical migrants were not clearly demonstrated in this study.

In large tracts of old-growth forests of the Cheat Mountains, West Virginia, species richness and abundance of neotropical migrants declined between 1947 and 1983 (Hall 1984). Populations of Solitary Vireo, Magnolia Warbler, Blackburnian Warbler, and Canada Warbler decreased, while densities of Black-throated Blue Warblers remained relatively constant, and Black-throated Green Warblers increased. But, while more species declined than increased in a manner similar to that at Hubbard Brook, reduction in study plot size, winter blowdown of trees, closing of canopy gaps, forest succession, and loss of red spruce may explain such trends (Askins et al. 1990).

Two 10 to 11-ha plots, one in old-growth forest and one in second-growth habitat, were censused from 1965 to 1988 in a 1,550-ha forest preserve in northwestern Connecticut (Egler and Niering 1976; Magee 1965a,b). At both sites, the overall abundance of neotropical migrants increased, but densities of short-distance migrants and

permanent residents stayed relatively stable. Only one species of neotropical migrant declined. Though opening of the canopy may account for some of the population increases at the old-growth site, habitat changes do not readily explain the parallel increases at the second-growth site.

In 9 of 10 sites in the Great Smoky Mountains National Park, the total number of neotropical migrants did not differ between Fawver's 1947–1948 censuses and Wilcove's (1988) 1982–1983 surveys. Though individual species of neotropical migrants declined at various sites, the declines were not consistent across sites.

A fifth study by Baird (1990), published after the review by Askins and his colleagues, compared bird censuses from 1930 and 1931 to censuses repeated in 1983, 1984, and 1985 in a 6,877-ha forest tract of Allegany State Park, New York. Baird detected a 14.5% decline in forest bird species but emphasized that forest maturation, deer browsing, and loss of farming readily explained most population changes of individual species.

Consequently, data from extensive forest tracts failed to conclusively resolve the suspicion that neotropical migrants have experienced a widespread decline in abundance. Unfortunately, a persistent decline caused by large-scale processes like conversion of tropical forests may be masked by drastic local declines on the breeding grounds (Askins et al. 1990). Though a shortage of long-term regional census data has greatly impeded assessments of continental trends in nongame bird populations, the Breeding Bird Survey (BBS) coordinated by the U.S. Fish and Wildlife Service and Canadian Wildlife Service was designed to fill this gap. Recent compilations of BBS data offer fresh insights about general population fluctuations of neotropical migrants in eastern North America.

Regional Trends Based on Breeding Bird Survey Data

BBS trend data were summarized for 230 North American species for the period 1966–1979 (Robbins et al. 1986), and more recently, for eastern species up to 1987 (Robbins et al. 1989a). Between 1966 and 1978, populations of 75% of the 62 neotropical migrant species were stable or increasing, and 18 of the 23 species with significant trends exhibited increases. In contrast, during the late (1978–1987) period, 75% of the forest neotropical migrants displayed negative trends, and 20 of 25 species showing significant trends had declining populations. No significant pattern was detected in permanent residents and short-distance migrants, suggesting that the consistent trends in long-distance migrants were unrelated to biases (e.g., variable ability and number of volunteers; nonrandom habitat changes along census roads) of the survey method itself. Analyzing continent-wide BBS data, Sauer and Droege (in press) also reported recent (1978–1988) population decreases (fig. 1), particularly in eastern birds and forest-breeding birds (fig. 2). However, after summarizing the rises and falls in populations over a longer period of time (1966–1988) (fig. 3), Sauer and Droege concluded that overall trends of neotropical migrants were generally stable or increasing. In contrast to neotropical migrants, short-distance and resident species nesting in grasslands and scrublands showed consistent population declines over the longer BBS period (Droege and Sauer 1990), possibly in relation to patterns of drought and population trends of the parasitic Brown-headed Cowbird.

The period of increase in neotropical migrants from 1966 to 1979 may reflect the large-scale adjustment of breeding birds to increasing amounts of mature eastern

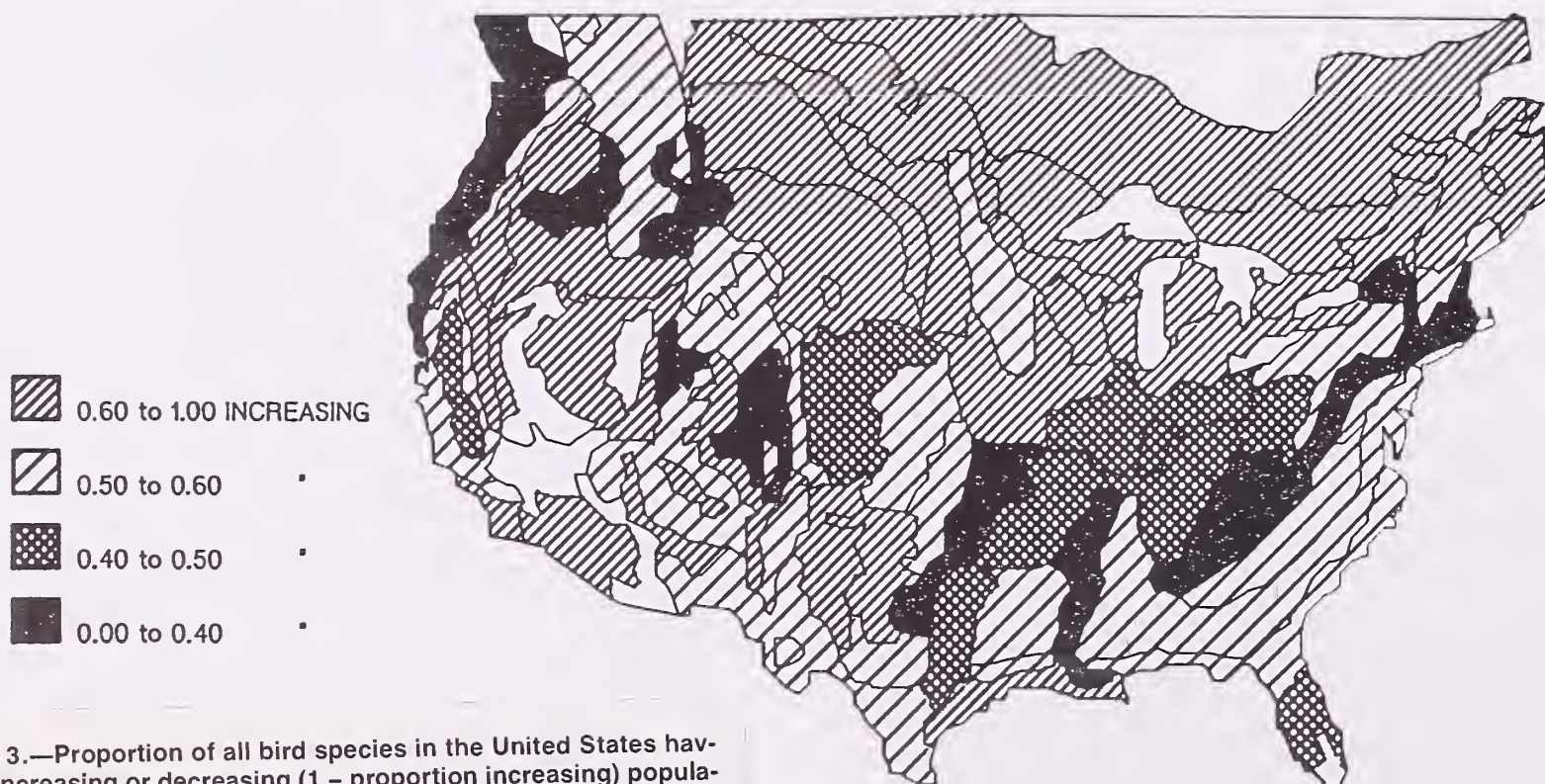


Figure 3.—Proportion of all bird species in the United States having increasing or decreasing (1 – proportion increasing) populations during the 1966 to 1988 period of the Breeding Bird Survey. (Courtesy Sam Droege, Office of Migratory Bird Management, U.S. Fish and Wildlife Service.)

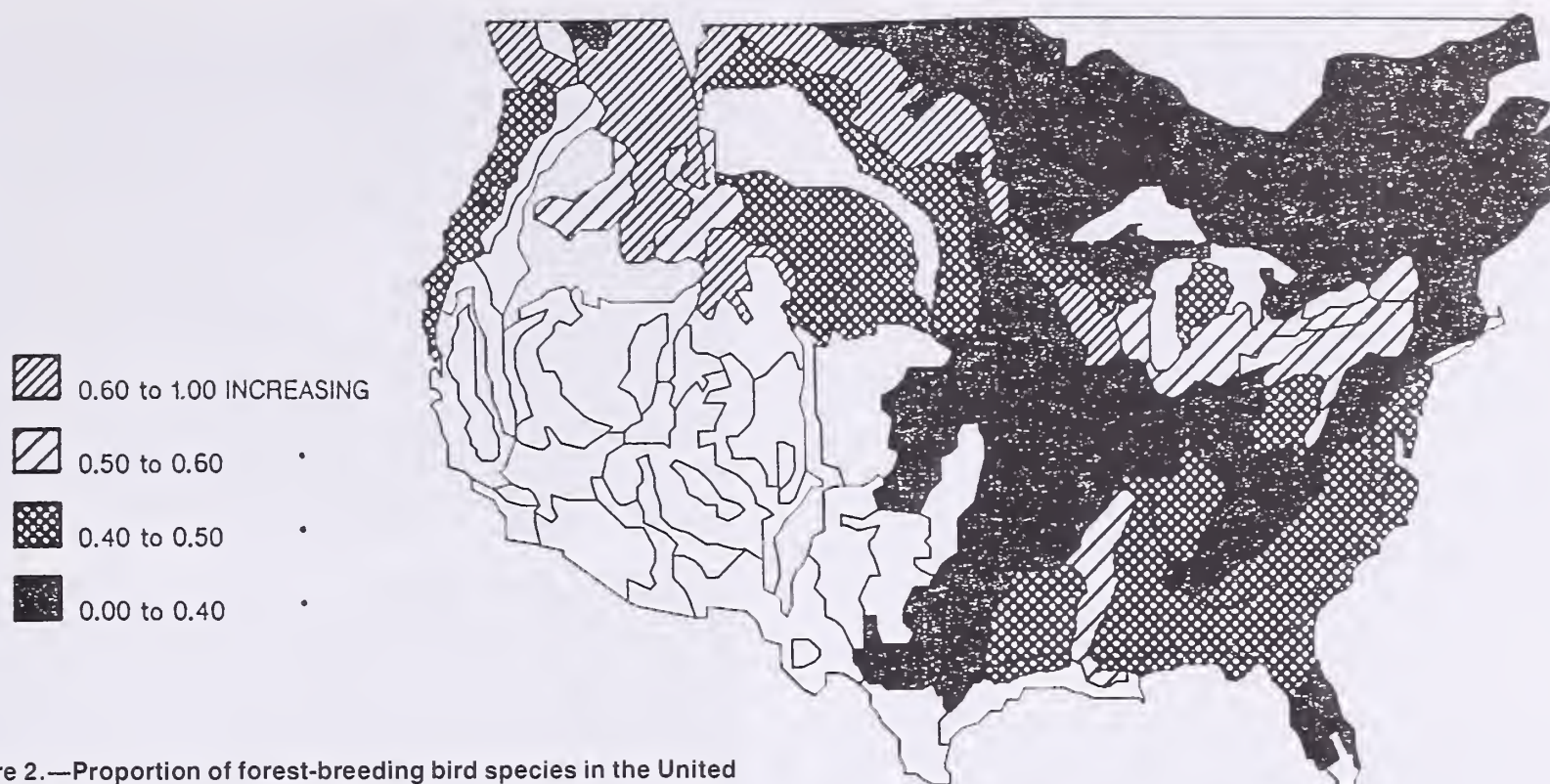


Figure 2.—Proportion of forest-breeding bird species in the United States having increasing or decreasing (1 – proportion increasing) populations during the 1978 to 1988 period of the Breeding Bird Survey. Areas that were undersampled ($N < 4$) are clear (not filled in) on map. (Courtesy Sam Droege, Office of Migratory Bird Management, U.S. Fish and Wildlife Service.)

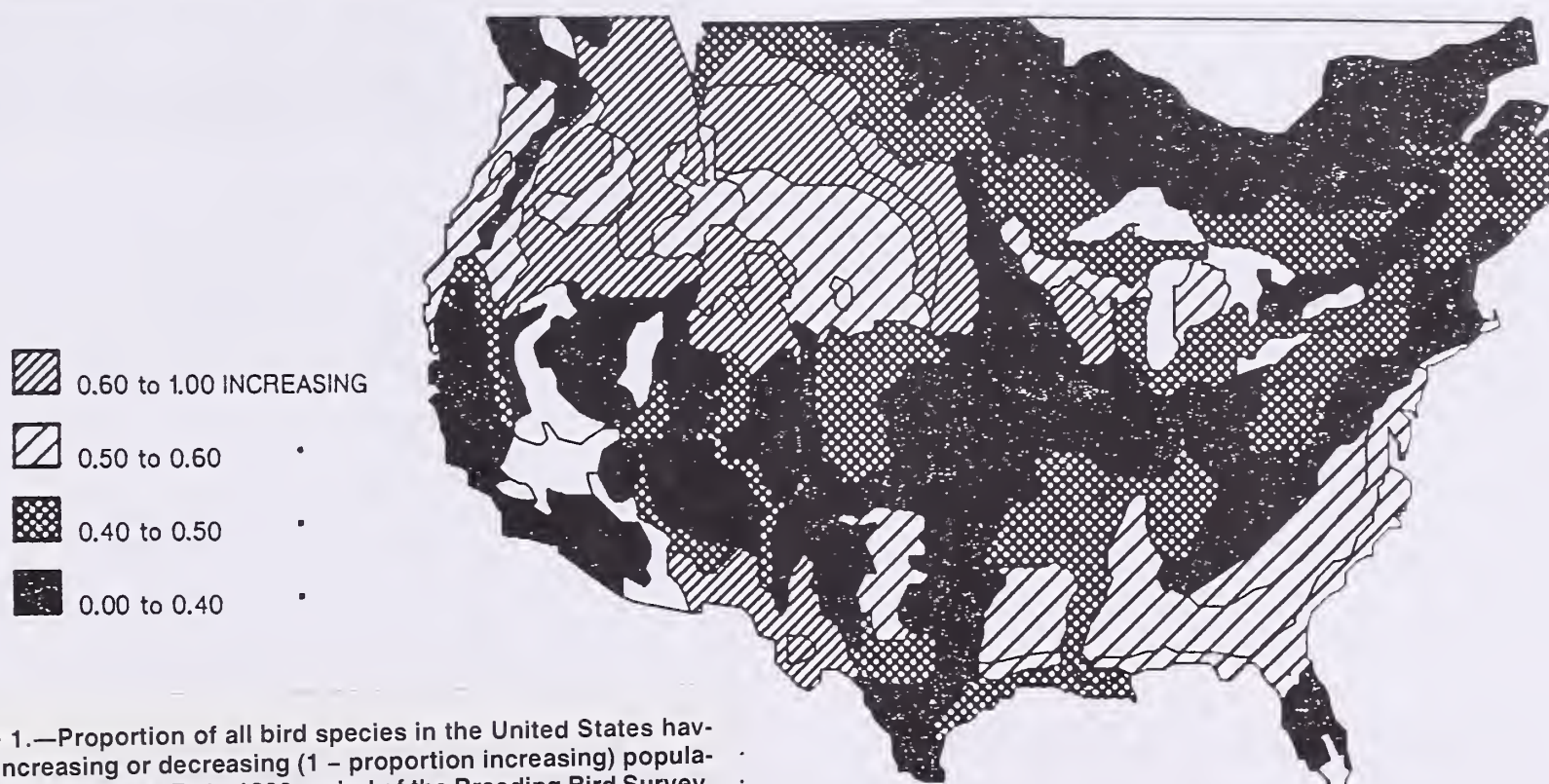


Figure 1.—Proportion of all bird species in the United States having increasing or decreasing (1 – proportion increasing) populations during the 1978 to 1988 period of the Breeding Bird Survey. (Courtesy Sam Droege, Office of Migratory Bird Management, U.S. Fish and Wildlife Service.)

forests (Birch 1989, Birch and Wharton 1982, Brooks and Birch 1988), while the recent declines may be related to accelerating deforestation rates in the Andes and on the Caribbean slope of Central America (e.g., Gradwohl and Greenberg 1988, Sader and Joyce 1988). This argument is compatible with Rappole and Powell's (1986) hypothesis that habitat limitation for forest migrants will shift from the breeding to the wintering grounds as more

tropical forests are destroyed and recovery rates of North American forests decline.

To determine whether patterns in abundances of migrant species were related to patterns of habitat use on the wintering grounds, Robbins et al. (1989a) tested the null hypothesis that the rate of population change in BBS data remains constant among migrant species using tropical scrub and forest habitats. While 8 of 12

open-scrub species that pass through or winter in the Sian Ka'an Biosphere Reserve of Mexico had positive slope changes, all 16 species of forest migrants using the reserve showed negative or zero changes in slope. To verify this pattern, Askins et al. (1990) classified forest neotropical migrants that breed in the eastern BBS region and generalized BBS results to encompass other tropical areas. After excluding species that specialize on caterpillar eruptions and bottomland gallery forests (i.e., where local deforestation is unlikely), Askins et al. confirmed that the overall pattern, i.e., declines in species using tropical forests, was essentially the same as that detected by Robbins and his colleagues. Consistent relationships between breeding bird trends and winter habitat use reinforce the premise that factors operating on the wintering grounds affect breeding season populations.

Conflicting Evidence

Population trends in forest-dwelling neotropical migrants have not been consistent among studies even when the same data sources are used. Using data from 12 BBS routes established in a coastal strip from Boston, Massachusetts, to Penobscot, Maine, Witham and Hunter (in press) compared population trends of 55 species to habitat trends estimated from aerial photographs. During the periods 1962–1966 and 1985–1987, only 3 of 16 forest-breeding neotropical migrants showed significant declines. In contrast, 11 of 17 short-distance migrants that breed in edge or open habitats or generalize in habitat use declined during the 1985–1987 period. Witham and Hunter suggest that declines in edge/open species were related to habitat changes on the breeding grounds (e.g., decreased amounts of nonforest upland, agricultural land, and forest) and advocated increased conservation attention to birds breeding in open and early successional habitats.

Based on analyses of Breeding Bird Census data from 13 sites throughout the eastern United States, Johnston and Hagan (in press) found that numbers of neotropical migrants were positively correlated with numbers of short-distance migrants and resident birds, implying that similar factors affected both groups of species. Since 1980, increases or no changes were detected in both groups at almost all sites.

Recent Evidence Based on Migration Count Data

Gauthreaux's (in press) analysis of long-term changes in the frequency of trans-Gulf flights provides some of the best evidence of reductions in migration volume. Using data from early (1965–1967) and recent (1987–1989) spring migration flights recorded at two weather radar stations in Lake Charles, Louisiana (example of radar images, fig. 4), and Galveston, Texas, Gauthreaux found a 50% reduction in the frequency (number of days) of flights. Declines were greatest in early migration (March 15–31), suggesting that early-arriving species have been most impacted.

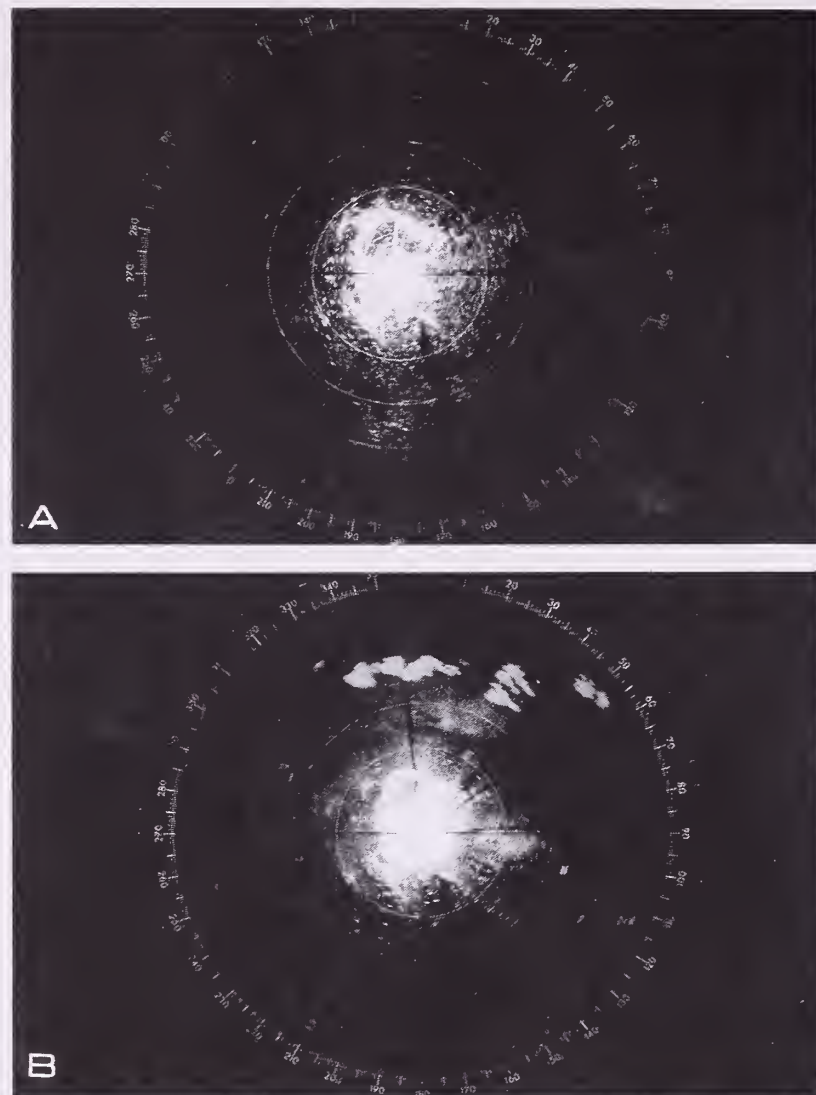


Figure 4.—Photographs of the radar screen of the WSR-57 radar at New Orleans, Louisiana, showing the spring arrival (photo A) and fall departure (photo B) of trans-Gulf migrants during daylight hours. The echoes (small dots) in the photographs represent individual flocks of birds migrating north (A) or south (B). Gaps in the echo patterns signify areas where migrants are landing, for example, along the Mississippi Gulf Coast. (Courtesy Sidney A. Gauthreaux, Jr., Department of Biological Sciences, Clemson University, Clemson, South Carolina.)

Using capture data from a migration banding station in Long Point, Ontario, Hussell et al. (in press) reported that recent (1980's) declines of 21 species monitored over a 28-yr period (1961–1988) were associated with migratory status, with more long-distance migrants decreasing and more short-distance migrants increasing. Finding, however, that long-term data from two migration banding stations in the eastern United States were not consistently correlated with each other or with BBS trend data, Hagan et al. (in press) cautioned that migration count data should be used as a corroborative rather than as an absolute source of data and that data interpretation should be restricted to applicable geographic areas.

Summary of Negative and Positive Evidence

Several lines of evidence strongly imply that forest-dwelling long-distance migrants have declined in abundance: the same sets of species declined in several in-

dependent small forests; two region-wide analyses of eastern BBS data showed recent declines in forest migrants; and migration volume over the Gulf has decreased by half since the mid-1960's. On the other hand, the assumption that long-distance migrants have experienced widespread declines is not supported by the studies that show: erratic or stable trends in migrant populations in large forest tracts; inconsistencies in bird count data from different banding stations; and BBS trends that show long-term stability of total or regional populations. Some recent BBS studies additionally suggest that migrants and residents breeding in open habitats are experiencing more problems than forest species. When faced with conflicting evidence, most researchers would agree that developing a conservation program based on the assumption that birds have really declined is a safer and wiser strategy than ignoring what could turn out to be a disastrous problem. This viewpoint is advocated because of the obstacles and errors involved in detecting reductions in global populations.

Problems of Interpretation

Wilcove and Terborgh (1984) identified several major difficulties in detecting widespread population declines. Theoretically, a given species may express a widespread reduction in its population by contracting its geographical range, by occupying fewer habitats within a region, by declining in abundance in some or all habitats, or by using a combination of these responses. Because of differences in species-specific life histories, ecologies, and responses to disturbance, population changes may be more visible or detectable in some species than in others. The detrimental effects of habitat disturbance in the Neotropics may be diffused across the entire breeding range in some species because of winter intermixing of races and higher winter densities per unit area (Rappole et al. 1983). Also, the existence of nonbreeding, nonterritorial individuals in some populations ("floaters") could obscure or mask sudden declines in densities of territorial birds if they replaced vacancies left by previous territory holders.

Other problems involve biases and "noise" related to the count method. For instance, canopy-using birds, many of which are migratory, are underrepresented in mist net captures (Lack and Lack 1972), making comparisons across habitats difficult. To estimate the number of breeding pairs, spot-map methods rely on counts of singing males. Consequently, density estimates may be inflated because of recorded detections of unmated males. Based entirely on roadside bird counts conducted by volunteers, BBS estimates are distrusted by many ornithologists. Sufficiently large samples of population counts from representative habitats throughout a species range will solve the "noise" problem, and temporal and spatial standardization of sampling effort and methodology should control for most biases (Askins et al. 1990). Under conditions of grave environmental or public health threat, Askins et al. (1990) recommend that the level of statistical significance for detecting changes be

greater than 0.05 (e.g., 0.1). This would reduce the probability of making Type II errors (overlooking real population declines) while ensuring a reasonable level of statistical rigor.

FACTORS SUSPECTED TO BE RESPONSIBLE FOR DECLINES

Forest Fragmentation on the Breeding Grounds

Though long-term studies of bird populations in small, isolated forest patches revealed consistent declines in some species and local extinctions in others, similar population trends were not observed in large forest blocks (Askins et al. 1990). This lack of similarity in results may be partially explained by the relationship between bird community composition and size of forest stand.

Relationships Among Forest Area, Isolation, and Species Use

Owing to increased species richness of edge and interior-edge birds in small, isolated patches, the total number of species per unit area is sometimes unrelated or negatively related to forest area (Askins et al. 1987, Blake and Karr 1984, Lynch and Whigham 1984, Whitcomb et al. 1981). But more species of forest-interior birds—the majority being neotropical migrants—tend to be found in larger forests than in small forests, and some of these species decline in abundance or disappear in small forest patches (e.g., Ambuel and Temple 1983, Askins et al. 1987, Blake and Karr 1984, Freemark and Merriam 1986, Howe 1984). Increased sampling effort in large forests increases the probability of detecting more species, particularly if some are rare. When this bias is controlled, a positive relationship between forest area and overall species richness is detected in some studies (Askins et al., in press; Forman et al. 1976; Howe 1984), but not in others (Blake and Karr 1984). Blake and Karr (1984) showed that one large forest sustains fewer bird species than two forests of the same total area, but even so, the species richness of neotropical migrants and forest-interior birds was higher in the single large forest.

Species whose densities are consistently higher per unit area in extensive forest tracts than in small ones may be "area-sensitive," i.e., disproportionately sensitive to reductions in forest size (Temple 1986). Askins et al. (1987) demonstrated that the smallest forest size for some species was significantly larger than that expected by chance. Rather than total forest area, the size of the forest interior or "core area" was a better predictor of population variation of 16 bird species in 49 Wisconsin forests (Temple 1986). Large forests with small core areas owing to their elongated or irregular shapes may be relatively poor habitats for forest-interior or neotropical migrant species but excellent habitats for edge-affiliated species.

High correlations between isolation distance and forest area make it difficult to separate the individual effects of these two variables (Whitcomb et al. 1981). When the effect of forest area is removed statistically, isolated forest stands have significantly fewer forest-interior species than stands closer to other forests (Askins et al. 1987, Lynch and Whigham 1984, Whitcomb et al. 1981; but see Ambuel and Temple 1983, Blake and Karr 1987).

Structure, Composition, and Heterogeneity of Habitats

The abundances of individual species of forest-interior and neotropical migrants are often more closely associated with specific measures of habitat structure and composition than with forest area, but the overall abundance and species richness of these birds are usually more highly correlated with forest area (Askins et al. 1987, Blake and Karr 1987). Using multiple regression analysis, Ambuel and Temple (1983) and Blake and Karr (1987) also found that habitat heterogeneity (horizontal diversity of vegetation) was secondary to forest area as a predictor of species richness for forest-interior birds or uncommon neotropical migrants, and that it was unrelated to forest area. Freemark and Merriam (1986) determined that habitat heterogeneity was a superior predictor for species richness of forest-edge birds, but forest area was better for predicting richness of forest-interior birds and neotropical migrants.

To summarize, total densities and species richness of forest-interior birds and neotropical migrants are often greater per unit area in larger forests, but the occurrences of many individual species depend on characteristics of vegetation structure, composition, or diversity.

Why Are Small or Fragmented Forests Unfavorable?

The island biogeography model (MacArthur and Wilson 1967) has frequently been used to explain variation in numbers of bird species in habitat patches that differ in area and isolation (Diamond and May 1976, Forman et al. 1976, Wilson and Willis 1975). According to this model, stochastic changes in the populations that inhabit small habitat "islands" lead to local species extinctions because island populations are relatively small, with high extinction rates and low immigration rates. Though the positive relationship between species richness of forest-interior birds and forest area is consistent with this model (Whitcomb et al. 1981), unfavorable environmental conditions or biotic interactions may also explain why some forest-interior species are absent from small forests (Ambuel and Temple 1983).

Nests situated along forest edges and in small forest patches experience greater rates of nest predation (Wilcove 1985, Wilcove et al. 1986, Yahner and Scott 1988) and brood parasitism by Brown-headed Cowbirds (Brittingham and Temple 1983, Gates and Gysel 1978, Temple and Cary 1988) than those located in forest interiors.

Higher densities of nests along the forest edge, as observed by Gates and Gysel (1978), may result in increased predator densities or predator search effort in edge habitats. Unfavorable nesting conditions in small forests, i.e., those consisting largely of edge, may discourage habitat occupancy by susceptible bird species. Because forest-interior species tend to nest on or near the ground, to use open rather than cavity nests, and to have low clutch sizes and numbers of broods per year (Greenberg 1980, Whitcomb et al. 1981), they may be especially sensitive to high rates of nest predation and brood parasitism (Askins et al. 1990). Though some neotropical migrant species that nest on the ground (e.g., Ovenbird, Kentucky Warbler) are apparently less vulnerable to brood parasitism than others (e.g., Wood Thrush) (Robinson, in press), their young may suffer high predation rates in edge forests after fledging from the nest. Thus, while small habitat patches may serve as "sinks" for attracting birds, they may be unsuitable for successful reproduction by many neotropical migrants (Robinson 1988, in press).

Using data on productivity rates of 13 forest-interior species nesting at different distances from the forest edge, Temple and Cary (1988) modeled reproductive responses to simulated effects of forest fragmentation. They found that as the amount of forest edge expanded in relation to increasing fragmentation, overall fecundity declined until fragmentation was so severe that populations of forest-interior species became locally extinct. The model showed that impaired reproduction in a fragmented landscape could generate population declines and shifts in distribution of forest-interior species similar to those observed in actual fragmented forests. Consequently, increased rates of cowbird parasitism and predation in edge habitats may ultimately explain population declines. Rates of interaction may be greater in edge habitats than in forest interiors due to increased densities or adeptness of predators or parasites, or due to environmental factors (e.g., habitat surrounding the nest site) that facilitate rather than discourage interference.

While demographic factors such as mating success, adult survival and return rates, and mortality, dispersal, and recruitment rates of fledglings may critically influence population sizes in small and large forests, this information is unavailable for most neotropical migratory species. Population growth in small, isolated populations may be greatly inhibited by the ability of breeding birds to find mates. Probst and Hays (1987) attributed slow recovery of Kirtland's Warbler populations to reduced pairing success in marginal habitats. Gibbs and Faaborg (1990) found that only 25% of male Ovenbirds (an area-sensitive species) using small forest remnants (<140 ha) were mated whereas 75% of those occupying large, contiguous forest tracts (>500 ha) had mates. In contrast, proportions of paired and unpaired males of the Kentucky Warbler, a species thought to be more tolerant of habitat fragmentation, were equal between small and large forests. Furthermore, Faaborg et al. (1989) discovered a positive relationship between population size and mating success in Ovenbirds breeding

in two 300-ha forest "islands" and one large forest "mainland." Faaborg et al. (1989) speculated that the relationships between mating success, population size, and forest area were caused by edge-related conditions such as habitat variation, predation, and brood parasitism.

Although the predation and brood parasitism hypotheses are the only proposals clearly supported by experimental and observational evidence, other biotic interactions may also play critical roles in determining presence and abundance of neotropical migrants in different-sized forests. For example, losses of forest-interior species from forest remnants may conceivably involve competitive interactions with edge species for food (Butcher et al. 1981), nest sites, or predator-free space. Askins and Philbrick (1987) found that the abundance of forest neotropical migrants was significantly negatively associated with the abundance of suburban, i.e., edge, species, but this pattern may merely reflect differences in responses of group members to habitat changes.

Data are lacking to support or refute the hypothesis that more neotropical migrant species reside in large than small areas because larger areas contain a wider array of limited habitats that may attract habitat specialists. Also, if patterns of abundance and distribution of neotropical migrants are associated with land coverages larger than a forest tract, then interpretations of population responses to forest fragmentation may differ in relation to scale of observation.

Interpretations Vary with Scale and Geography

Lack of information at the wide landscape scale hinders interpretation of regional declines. In a recent comparison of two agricultural landscapes near Ottawa, Canada, Freemark (in press) determined that total species richness was higher in the landscape that was more forested and more interconnected. Taking this one step further, Villard et al. (in press) developed a landscape model that predicted a pattern of "winking patches" whereby populations of habitat patches become extinct and are recolonized, with dynamic stability at a higher metapopulation level. In sets of 72 and 16 forest patches, the frequency of patch occurrence in three neotropical migrant species (Wood Thrush, Ovenbird, and Scarlet Tanager) did not significantly differ between years because the total number of recolonizations across the entire landscape balanced the number of local extinctions. Given this result, Villard et al. suggested that the relevant demographic unit for these species in fragmented landscapes consists of a network of interacting subpopulations, rather than an array of isolated populations exposed to independent events.

Geographical differences in land use practices and impacts may account for some variation in population trends, yet these differences have rarely been teased apart. Using new methods to analyze BBS data for eight species of wood warblers, James et al. (in press) found

that population trends, while relatively similar among species, varied by physiographic strata (geographic units that are homogeneous in dominant vegetation and physiography) and by observational scale (e.g., within state, state, region). Such results suggest that conservation efforts should be focused 1) in physiographic regions or geographical areas where population declines are most severe, and 2) at levels of spatial resolution where processes causing population changes (e.g., land management actions) can be detected, monitored, and modified.

Clearly, tests of alternative hypotheses that focus on the relative roles of habitat quantity and quality, observational scale (e.g., local, landscape, state, region), density-dependent and biotic interactions, resource-management activities, and the ecologies and geographies of different species and groups of species, are critically needed before declines of migratory birds can be unequivocally attributed to local, regional, or tropical problems. Nevertheless, where data are accurate and extensive enough to suggest that individual species, sets of species, or geographical units are in jeopardy, the mobilization and monitoring of pilot management projects and conservation strategies are recommended.

Habitat Management for Forest-Interior Species

Enough consistent data have accumulated to suggest 1) that habitat fragmentation negatively affects populations of forest-interior migrants in eastern North America; 2) that several forest migrant species are area-sensitive, collectively fitting the definition of a "management indicator guild" or "response guild" (a group comprised of species that respond similarly to environmental changes resulting from resource-management practices); 3) that available data and models on the relationship between bird abundance and extent of forest size and isolation (e.g., Temple and Cary 1988, Robbins et al. 1989b) can be used to develop field strategies for managing groups of sensitive habitat-interior species; and 4) that the effectiveness of such models and strategies can be tested, verified, and improved with time. For instance, the findings of Robbins et al. (1989b) (e.g., table 1) can be field-tested by classifying species into guilds and then examining guild responses to habitat alterations caused by forest management practices. Though the concept of the management guild has been heavily criticized (Landres et al. 1988), it can be argued that the concept has not been properly tested. Typically, management guild composition has been predefined based on species similarities in microhabitat, food, or substrate selection rather than on how species respond to abrupt macrohabitat changes like those caused by forest fragmentation. Field implementation of a habitat management model for the forest-interior migrants group would provide an excellent opportunity for appropriately testing the management guild concept.

Table 1.—Forest areas at which the probability of occurrence (PO) is at maximum and at 50% of the maximum (suggested minimum area for breeding) for 26 species of area-sensitive birds, i.e., species whose probability of occurrence increases with area. Source Robbins et al. 1989b.^a

Species	Area (ha)		Area (ha) of 3 smallest isolated forests where a species was detected on ≥ 2 visits		
	Max. PO	50% PO			
Neotropical migrants					
Acadian Flycatcher	3,000 +	15.0	4.5	2.6	0.2
Great-crested Flycatcher	72	0.3	2.5	0.8	0.8
Blue-gray Flycatcher	3,000 +	15.0	23.0	10.1	6.8
Veery	250	20.0	24.1	11.3	9.3
Wood Thrush	500	1.0	0.8	0.8	0.2
Red-eyed Vireo	3,000 +	2.5	0.7	0.5	0.5
Northern Parula	3,000 +	520.0	516.0	415.0	10.1
Black-throated Blue Warbler	3,000 +	1,000.0	1,500.0	1,500.0	1,120.0
Cerulean Warbler	3,000 +	700.0	1,500.0	637.0	138.0
Black-and-white Warbler	3,000 +	220.0	493.0	208.0	208.0
Worm-eating Warbler	3,000 +	150.0	30.4	29.1	21.0
Ovenbird	450	6.0	2.5	1.2	0.8
Northern Waterthrush	3,000 +	200.0	187.0	187.0	24.1
Louisiana Waterthrush	3,000 +	350.0	184.1	24.7	24.7
Kentucky Warbler	300	17.0	11.0	10.4	9.3
Canada Warbler	3,000 +	400.0	883.0	883.0	187.0
Summer Tanager	3,000 +	40.0	47.8	47.8	24.7
Rose-breasted Grosbeak	3,000 +	1.0	123.0	24.1	11.3
Short-distance migrants					
Red-shouldered Hawk	3,000	225.0	52.0	40.5	39.7
American Crow	10	0.2	0.5	0.2	0.2
White-breasted Nuthatch	300	3.0	4.2	3.0	1.6
Permanent residents					
Red-bellied Woodpecker	85	0.3	1.8	1.6	0.2
Hairy Woodpecker	200	6.8	26.7	16.1	10.4
Pileated Woodpecker	3,000 +	165.0	65.2	64.3	42.2
Tufted Titmouse	52	0.5	0.8	0.6	0.2

^aTable 2 lists the scientific names of species.

Known and Potential Effects of Tropical Deforestation

Distribution of Neotropical Migrants in Winter

Of the migratory landbird species that breed in North America, approximately 160 winter **primarily south** of the United States (table 2), and about 100 others migrate to the southern United States as well as tropical or subtropical regions. Though wintering migrants commonly constitute 40–50% of the bird abundance in various habitats in Mexico, the Bahamas, and the Greater Antilles, the percentage decreases as distances from the United States increase (e.g., 20–40% in Guatemala and Belize, 10–30% in Costa Rica and Panama, 5–15% in Puerto Rico and Colombia, and about 1% in Ecuador, Peru, and Bolivia) (Terborgh 1980, 1989). The sizes and geographical locations of wintering ranges vary greatly among neotropical migrant species, but apparently high numbers of species are concentrated in northern Middle America and the Caribbean Islands (Rappole et al. 1983). Because of this channeling effect, densities of migrant species have been estimated to be 5–8 times higher on the wintering grounds than in breeding areas

(Morton 1980, Terborgh 1980). Though this latitudinal shift in densities was not detected in territorial American Redstarts and Black-throated Blue Warblers wintering in Jamaica (Holmes et al. 1989), few quantitative data are available for other species.

Current Rates of Forest Destruction

Tropical regions are undergoing rapid conversion from forested to open landscapes dominated by grasslands and agriculture (Gradwohl and Greenberg 1988, Keogh 1984, Myers 1980). Areas with some of the highest rates of deforestation—the Greater Antilles, Mexico, Central America, and northern South America—also have the greatest concentrations of migrants (Terborgh 1989). The annual rate of forest conversion in Central America (based on data gathered during the mid-1970's) ranges from 0.7% in Belize and Panama to 3.3% in El Salvador and 4% in Costa Rica (Gradwohl and Greenberg 1988, Lanly 1982). Analyses of satellite imagery reveal that more than 78% of the forest in the Tropical Wet Life Zones of Costa Rica has been lost (Sader and Joyce 1988). Some rare and unique forest types have all

Table 2.—Preliminary list of migrant landbird species that breed primarily in the Nearctic and winter generally south of the United States-Mexico border (modified from S. Droege and R. Greenberg, unpublished).^a Species that nest in cavities (C) (marked for Animal Inn Program) or that are federally listed as threatened, endangered (E), or candidate (C2, C3) species or subspecies (ss) are specified.

No.	Common name	Scientific name	Nest type	Federal list
1.	Turkey Vulture	<i>Cathartes aura</i>	C	
2.	Osprey	<i>Pandion haliaetus</i>		
3.	Mississippi Kite	<i>Ictinia mississippiensis</i>		
4.	Sharp-shinned Hawk	<i>Accipiter striatus</i>		
5.	Cooper's Hawk	<i>Accipiter cooperii</i>		
6.	Broad-winged Hawk	<i>Buteo platypterus</i>		
7.	Swainson's Hawk	<i>Buteo swainsoni</i>		C3c
8.	Am. Swallow-tailed Kite	<i>Elanoides forficatus</i>		
9.	American Kestrel	<i>Falco sparverius</i>		
10.	Merlin	<i>Falco columbarius</i>		
11.	Peregrine Falcon	<i>Falco peregrinus</i>		E
12.	Band-tailed Pigeon	<i>Columba fasciata</i>		
13.	Black-billed Cuckoo	<i>Coccyzus erythrophthalmus</i>		
14.	Yellow-billed Cuckoo	<i>Coccyzus americanus</i>		C3b
15.	Mangrove Cuckoo	<i>Coccyzus minor</i>		
16.	Flammulated Owl	<i>Otus flammeolus</i>	C	
17.	Burrowing Owl	<i>Athene cunicularia</i>		
18.	Common Nighthawk	<i>Chordeiles minor</i>		
19.	Lesser Nighthawk	<i>Chordeiles acutipennis</i>		
20.	Chuck-will's-Widow	<i>Caprimulgus carolinensis</i>		
21.	Whip-poor-will	<i>Caprimulgus vociferus</i>		
22.	Black Swift	<i>Cypseloides niger</i>		
23.	Chimney Swift	<i>Chaetura pelagica</i>	C	
24.	Vaux's Swift	<i>Chaetura vauxi</i>	C	
25.	White-throated Swift	<i>Aeronautes saxatalis</i>		
26.	Ruby-throated Hummingbird	<i>Archilochus colubris</i>		
27.	Black-chinned Hummingbird	<i>Archilochus alexandri</i>		
28.	Calliope Hummingbird	<i>Stellura calliope</i>		
29.	Broad-tailed Hummingbird	<i>Selasphorus platycercus</i>		
30.	Rufous Hummingbird	<i>Selasphorus rufus</i>		
31.	Allen's Hummingbird	<i>Selasphorus sasin</i>		
32.	Belted Kingfisher	<i>Ceryle alcyon</i>		
33.	Red-naped Sapsucker	<i>Sphyrapicus nuchalis</i>	C	
34.	Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	C	
35.	Williamson's Sapsucker	<i>Sphyrapicus thyroides</i>	C	
36.	Olive-sided Flycatcher	<i>Contopus borealis</i>		
37.	Western Wood-Pewee	<i>Contopus sordidulus</i>		
38.	Eastern Wood-Pewee	<i>Contopus virens</i>		
39.	Yellow-bellied Flycatcher	<i>Empidonax flaviventris</i>		
40.	Acadian Flycatcher	<i>Empidonax virens</i>		
41.	Alder Flycatcher	<i>Empidonax alnorum</i>		
42.	Willow Flycatcher	<i>Empidonax traillii</i>		C2(ss)
43.	Least Flycatcher	<i>Empidonax minimus</i>		
44.	Hammond's Flycatcher	<i>Empidonax hammondi</i>		
45.	Dusky Flycatcher	<i>Empidonax oberholseri</i>		
46.	Gray Flycatcher	<i>Empidonax wrightii</i>		
47.	Western Flycatcher	<i>Empidonax difficilis</i>	C	
48.	Eastern Phoebe	<i>Sayornis phoebe</i>		
49.	Say's Phoebe	<i>Sayornis saya</i>		
50.	Ash-throated Flycatcher	<i>Myiarchus cinerascens</i>	C	
51.	Great-crested Flycatcher	<i>Myiarchus crinitus</i>	C	
52.	Western Kingbird	<i>Tyrannus verticalis</i>		
53.	Eastern Kingbird	<i>Tyrannus tyrannus</i>		
54.	Gray Kingbird	<i>Tyrannus dominicensis</i>		
55.	Cassin's Kingbird	<i>Tyrannus vociferans</i>		
56.	Scissor-tailed Flycatcher	<i>Tyrannus forficatus</i>		
57.	Purple Martin	<i>Progne subis</i>	C	
58.	Tree Swallow	<i>Tachycineta bicolor</i>	C	
59.	Violet-green Swallow	<i>Tachycineta thalassina</i>	C	
60.	Northern Rough-winged Swallow	<i>Stelgidopteryx serripennis</i>		
61.	Bank Swallow	<i>Riparia riparia</i>		
62.	Cliff Swallow	<i>Hirundo pyrrhonota</i>		
63.	Barn Swallow	<i>Hirundo rustica</i>		
64.	House Wren	<i>Troglodytes aedon</i>	C	

Table 2.—Continued

No.	Common name	Scientific name	Nest type	Federal list
65.	Ruby-crowned Kinglet	<i>Regulus calendula</i>		
66.	Blue-gray Gnatcatcher	<i>Polioptila caerulea</i>		
67.	Veery	<i>Catharus fuscescen</i>		
68.	Gray-cheeked Thrush	<i>Catharus minimus</i>		
69.	Swainson's Thrush	<i>Catharus swainsonii</i>		
70.	Hermit Thrush	<i>Catharus guttatus</i>		
71.	Wood Thrush	<i>Hylocichla mustelina</i>		
72.	American Robin	<i>Turdus migratorius</i>		
73.	Gray Catbird	<i>Dumetella carolinensis</i>		
74.	Water Pipit	<i>Anthus spinoletta</i>		
75.	Sprague's Pipit	<i>Anthus spragueii</i>		
76.	Cedar Waxwing	<i>Bombycilla cedrorum</i>		
77.	White-eyed Vireo	<i>Vireo griseus</i>		
78.	Bell's Vireo	<i>Vireo bellii.</i>		E(ss)
79.	Black-capped Vireo	<i>Vireo atricapillus.</i>		E
80.	Gray Vireo	<i>Vireo vicinior</i>		
81.	Solitary Vireo	<i>Vireo solitarius</i>		
82.	Yellow-throated Vireo	<i>Vireo flavifrons</i>		
83.	Warbling Vireo	<i>Vireo gilvus</i>		
84.	Philadelphia Vireo	<i>Vireo philadelphicus</i>		
85.	Red-eyed Vireo	<i>Vireo olivaceus</i>		
86.	Black-whiskered Vireo	<i>Vireo altiloquus</i>		
87.	Bachman's Warbler	<i>Vermivora bachmanii.</i>		E
88.	Blue-winged Warbler	<i>Vermivora pinus</i>		
89.	Golden-winged Warbler	<i>Vermivora chrysoptera</i>		
90.	Tennessee Warbler	<i>Vermivora peregrina</i>		
91.	Orange-crowned Warbler	<i>Vermivora celata</i>		
92.	Nashville Warbler	<i>Vermivora ruficapilla</i>		
93.	Virginia's Warbler	<i>Vermivora virginiae.</i>	C	
94.	Lucy's Warbler	<i>Vermivora luciae.</i>	C	
95.	Northern Parula	<i>Parula americana</i>		
96.	Yellow Warbler	<i>Dendroica petechia</i>		
97.	Chestnut-sided Warbler	<i>Dendroica pensylvanica</i>		
98.	Magnolia Warbler	<i>Dendroica magnolia</i>		
99.	Cape May Warbler	<i>Dendroica tigrina</i>		
100.	Black-throated Blue Warbler	<i>Dendroica caerulescens</i>		
101.	Black-throated Gray Warbler	<i>Dendroica nigrescens</i>		
102.	Townsend's Warbler	<i>Dendroica townsendi</i>		
103.	Hermit Warbler	<i>Dendroica occidentalis</i>		
104.	Black-throated Green Warbler	<i>Dendroica virens</i>		
105.	Golden-cheeked Warbler	<i>Dendroica chrysoparia.</i>		E
106.	Blackburnian Warbler	<i>Dendroica fusca</i>		
107.	Yellow-throated Warbler	<i>Dendroica dominica</i>		
108.	Grace's Warbler	<i>Dendroica graciae</i>		
109.	Pine Warbler	<i>Dendroica pinus</i>		
110.	Kirtland's Warbler	<i>Dendroica kirtlandii.</i>		E
111.	Prairie Warbler	<i>Dendroica discolor</i>		
112.	Palm Warbler	<i>Dendroica palmarum</i>		
113.	Bay-breasted Warbler	<i>Dendroica castanea</i>		
114.	Blackpoll Warbler	<i>Dendroica striata</i>		
115.	Cerulean Warbler	<i>Dendroica cerulea</i>		
116.	Black-and-white Warbler	<i>Mniotilta varia</i>		
117.	American Redstart	<i>Setophaga ruticilla</i>		
118.	Prothonotary Warbler	<i>Protonotaria citrea.</i>	C	
119.	Worm-eating Warbler	<i>Helmitheros vermivorus</i>		
120.	Swainson's Warbler	<i>Limnithlypis swainsonii</i>		
121.	Ovenbird	<i>Seiurus aurocapillus</i>		
122.	Northern Waterthrush	<i>Seiurus noveboracensis</i>		
123.	Louisiana Waterthrush	<i>Seiurus motacilla</i>		
124.	Kentucky Warbler	<i>Oporornis formosus</i>		
125.	Connecticut Warbler	<i>Oporornis agilis</i>		
126.	Mourning Warbler	<i>Oporornis philadelphia</i>		
127.	MacGillvray's Warbler	<i>Oporornis tolmiei</i>		
128.	Common Yellowthroat	<i>Geothlypis trichas</i>		
129.	Hooded Warbler	<i>Wilsonia citrina</i>		
130.	Wilson's Warbler	<i>Wilsonia pusilla</i>		
131.	Canada Warbler	<i>Wilsonia canadensis</i>		
132.	Yellow-breasted Chat	<i>Icteria virens</i>		

Table 2.—Continued

No.	Common name	Scientific name	Nest type	Federal list
133.	Summer Tanager	<i>Piranga rubra</i>		
134.	Scarlet Tanager	<i>Piranga olivacea</i>		
135.	Western Tanager	<i>Piranga ludoviciana</i>		
136.	Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>		
137.	Black-headed Grosbeak	<i>Pheucticus melanocephalus</i>		
138.	Blue Grosbeak	<i>Guiraca caerulea</i>		
139.	Lazuli Bunting	<i>Passerina amoena</i>		
140.	Indigo Bunting	<i>Passerina cyanea</i>		
141.	Painted Bunting	<i>Passerina ciris</i>		
142.	Dickcissel	<i>Spiza americana</i>		
143.	Green-tailed Towhee	<i>Pipilo chlorurus</i>		
144.	Chipping Sparrow	<i>Spizella passerina</i>		
145.	Clay-colored Sparrow	<i>Spizella pallida</i>		
146.	Brewer's Sparrow	<i>Spizella breweri</i>		
147.	Black-chinned Sparrow	<i>Spizella atrogularis</i>		
148.	Vesper Sparrow	<i>Pooecetes gramineus</i>		
149.	Lark Bunting	<i>Calamospiza melanocorys</i>		
150.	Savannah Sparrow	<i>Passerculus sandwichensis</i>		
151.	Baird's Sparrow	<i>Ammodramus bairdii</i>		
152.	Grasshopper Sparrow	<i>Ammodramus savannarum</i>		
153.	Lincoln's Sparrow	<i>Melospiza lincolnii</i>		
154.	Bobolink	<i>Dolichonyx oryzivorus</i>		
155.	Red-winged Blackbird	<i>Agelaius phoeniceus</i>		
156.	Yellow-headed Blackbird	<i>Xanthocephalus xanthocephalus</i>		
157.	Brewer's Blackbird	<i>Euphagus cyanocephalus</i>		
158.	Brown-headed Cowbird	<i>Molothrus ater</i>		
159.	Orchard Oriole	<i>Icterus spurius</i>		
160.	Northern Oriole	<i>Icterus galbula</i>		

^aSeveral neotropical migrant species were added to the original Droege and Greenberg list.

but disappeared. For example, less than 1% of the dry forests of the Pacific slope of Central America remain (Janzen 1988). Moreover, deforestation rates may be increasing rather than stabilizing in some countries; increases in deforestation rates from 2% to as high as 17% have been documented for some forest types in Costa Rica (Sader and Joyce 1988).

The likelihood that a tropical forest will fully regenerate varies depending on the kind and amount of current land use. Up to 90% of the cleared tropical forest in Veracruz (Estrada and Coates-Estrada 1988) has been cleared for cattle-ranching, a prevalent land use in the Dominican Republic and the Andean countries as well. Forests are also converted to agricultural lands for use as small subsistence plots and as major commodity crops, including coffee, cacao, bananas, cotton, sugar cane, and palm oil. In some areas, abandonment of agricultural interests have led to a dramatic increase in secondary forest (e.g., Puerto Rico, Brash 1987).

While forest clearing for ranching and some agricultural crops eliminates the tree overstory altogether, shade canopies that tend to duplicate native forest conditions are required for some crops. Tree canopies have historically been used in coffee plantations (e.g., Brash 1987), but sun-tolerant strains of coffee are now being cultivated without shade trees in some localities (Askins et al. 1990). Wooded areas that are retained for shelterbelts, greenbelts, and hedgerows also supply valuable habitats for migrant species, but the extent that these remnants are left depends on their application. Other forestland

actions with unknown effects on migratory birds are large-scale reforestation with exotic pines and eucalyptus (Cruz and Fairbairn 1980), planting of woodlots, and introduction of agroforestry systems (Askins et al. 1990).

It is wise to keep in perspective that migratory birds and other biota in Mexico and Central America have had to accommodate a long history of human disturbance (Lynch 1989). The presence of hundreds of Maya ruins in Mexico's Yucatan Peninsula attest to the magnitude of past human endeavors. In the Petén of Guatemala, archaeological evidence suggests that forest clearing for agriculture was extensive (Deevey et al. 1979). In some Middle American regions, contemporary forest acreages may actually exceed amounts of forest cover at the height of the Classic Maya civilization, 1,000 to 1,500 years ago (Lynch 1989).

Habitat Use by Wintering Migrants

Numbers of wintering migrant species differ widely among habitat types (Hutto, in press; Lynch 1989), but of 332 nearctic migrant species that winter in the Neotropics, 107 (32%) occur in forests or woodlands (Rappole et al. 1983). While approximately half of the forest-associated migrants additionally use nonforest habitats, the rest winter exclusively in forests (Askins et al. 1990). Such forested habitats range from mature to second-growth forests, and from tropical broadleaf and subtropical evergreen to riparian, deciduous, and

coniferous/mixed forests (e.g., Hutto, in press; Lynch 1989).

While some migrant species reach peaks of abundance in undisturbed forests, second-growth forests and fallow fields provide valuable habitats to others (Hutto 1989, Lynch 1989, Martin 1985). For example, 63% of the migratory species surveyed at 36 sites in western Mexico were either restricted to, or more often detected in, second-growth habitat, while the remainder were found primarily in undisturbed forest (Hutto, in press). Lynch (1989) reported that species richness of both migrants and residents wintering in Mexico's Yucatan Peninsula was substantially higher in mist net samples from pastures and old brushy fields (known as "acahual") than in those from mature semi-evergreen forest. Because tropical second-growth forests older than 20 or 30 years are not representative of earlier seral stages, Askins et al. (1990) recommend that they not be classed with pastures that are frequently disturbed by grazing and burning. But, if active pastures and croplands contain wooded areas, even they are occupied by some forest migrants (Lynch, in press).

Specialization Versus Flexibility in Habitat Use

Some migratory species have been identified as highly flexible in winter habitat use, occupying a broad range of habitat types (Hutto 1986, 1988; Karr 1976; Lynch 1989), and responsive to temporal shifts in resource abundance (Leck 1972, Willis 1966). For example, mixed-species flocks in western Mexico are comprised of nomadic canopy-foraging insectivores, of which about half are migrant species (Hutto 1986). Yet, other species of neotropical migrants use habitat types selectively in winter (Lynch 1989; Powell et al., in press; Terborgh 1989; Waide 1980); are morphologically adapted to specialize on tropical food supplies (e.g., Greenberg 1987; Morton and Greenberg 1989; Rappole, in press); defend winter territories (e.g., Holmes et al. 1989, Rappole and Warner 1980, Rappole et al. 1989); and exhibit winter-site fidelity from year to year (Kricher and Davis 1986, Rappole et al. 1983).

Some overall patterns of habitat use are related to differences in species geographical ranges, in particular whether species reside and migrate in the East or West (Hutto 1986). For example, highly seasonal tropical environments are widely occupied by western migrants in Mexico and Costa Rica, but are mostly left vacant by eastern species in the Antilles and northern South America (Terborgh 1989). Several migrant species exhibit a seasonal switch in habitats (Robbins et al. 1989a), i.e., breeding in forest and wintering in scrub (Least Flycatcher, Eastern Wood-Pewee, Blue-gray Gnatcatcher, Rose-breasted Grosbeak) or breeding in scrub and wintering in forest (Chestnut-sided Warbler, Blue-winged Warbler, and White-eyed Vireo). Habitat segregation between sexes (e.g., Lynch et al. 1985, Morton et al. 1987) and age/behavior classes (e.g., territorial birds vs. floaters) further complicates interpretations of habitat use and specialization.

Because the degree of specialization in habitat choice obviously varies among wintering migrant species, their responses to habitat disturbance are likely to differ (Hutto, in press). While migrant species restricted to particular habitats and geographical areas may be severely jeopardized by tropical forest destruction and agricultural conversion, habitat generalists and nonterritorial species may show little or opposite responses. Forest specialists (e.g., Wood Thrush, Yellow-throated Vireo, Kentucky Warbler, Hooded Warbler, Black-and-white Warbler; Lynch 1989) are typically identified as species at greatest risk from tropical deforestation. But even migrant species associated with scrub thickets, second-growth forests, and wooded plantations may be vulnerable because of overall habitat loss caused by conversion to livestock pastures and croplands devoid of trees and shrubs (Askins et al. 1990; Powell et al., in press).

Clearly, more species-specific data on population trends, habitat requirements, geographical distributions, behavior, and demography are needed to identify those species at greatest risk on the wintering grounds. But, in the face of current rates of tropical deforestation, biologists and environmentalists are urging agencies, program managers, legislators, and publics at an international level to recognize that time is running out and that responsible steps for conserving species and restoring habitats are needed now (Janzen 1988; Morton and Greenberg 1989; Rappole, in press; Terborgh 1989). Thus, given the data currently available, prioritizing neotropical migrant species based on their relative susceptibility to extinction in wintering and breeding areas is a practical first step in conserving populations.

Species of concern were identified by Terborgh (1989) based on whether they winter in geographically restricted ranges and habitats. Terborgh's original list included 45 species (including 6 shorebirds), 26 of western or central affinities, 14 that breed primarily in the East, and 5 Arctic migrants. His assessment of sensitive migratory songbirds is given in table 3. Reed (in press) prioritized 47 warbler species and 10 vireo species using criteria related to habitat specificity, geographic range, and local population size. Six species, four federally listed as endangered (E), were identified by Reed as highly vulnerable to extinction on both their wintering and breeding grounds: Black-capped Vireo (E), Bachman's Warbler (E), Colima Warbler, Lucy's Warbler, Golden-cheeked Warbler (E), and Kirtland's Warbler (E). Reed additionally categorized Black-whiskered Vireo, Virginia's Warbler, Hermit Warbler, and Red-faced Warbler as high priority species on their breeding grounds, and Gray Vireo on its wintering grounds. Because neither Terborgh nor Reed incorporated information on current population trends, nesting limitations, productivity rates, rates of habitat loss, and population responses to land use actions, their species lists are fairly superficial, and, thus, more comprehensive efforts (e.g., Millsap et al. 1990) are needed to prioritize vulnerable species.

Effects of Habitat Loss on Winter Populations

There are few quantitative data on long-term population trends of neotropical migrants in wintering areas.

Table 3.—Terborgh's (1989) list of migrants (excluding waterfowl and shorebirds) having geographically restricted winter ranges.^a

Locality and Species	Principal natural habitat	Accepts disturbed habitat
Northern and central Mexico		
Black-chinned Hummingbird	Thorn scrub, galleries	Yes
Rufous Hummingbird	Pine-oak woodland	Yes
Allen's Hummingbird	Pine-oak woodland	?
Blue-throated Hummingbird	Pine-oak woodland	?
Botteri's Sparrow	Dry grassland	?
Western Mexico		
Calliope Hummingbird	Pine-oak woodland	?
Broad-billed Hummingbird	Thorn scrub, galleries	?
Dusky Flycatcher	Oak scrub	?
Gray Flycatcher	Arid scrub, galleries	Yes
Black-capped Vireo	Desert riparian	Yes
Bell's Vireo	Desert riparian	No
Gray Vireo	Arid scrub	?
Virginia's Warbler	Oak woodland	No
Colima Warbler	Pine-oak woodland	?
Lucy's Warbler	Desert riparian	No
Black-throated Gray Warbler	Oak woodland	Yes
Hermit Warbler	Fir forest	No
Red-faced Warbler	Pine oak woodland	No
Scott's Oriole	Desert scrub	?
Black-headed Grosbeak	Pine-oak woodland	Yes
Lazuli Bunting	Riparian woodland	?
Southeastern Mexico/Guatemala/Belize		
Swainson's Warbler	Evergreen forest	No
Blue-winged Warbler	Evergreen forest	?
Nashville Warbler	Evergreen forest	Yes
Golden-cheeked Warbler	Oak-juniper woods	No
Hooded Warbler	Evergreen forest	No
Greater Antilles and Bahamas		
Bachman's Warbler	Evergreen forest	?
Kirtland's Warbler	?	?
Cape May Warbler	Evergreen forest	Yes
Black-throated Blue Warbler	Evergreen forest	Yes
Prairie Warbler	Deciduous forest	Yes
Southern Central American lowlands		
Scissor-tailed Flycatcher	Deciduous forest	Yes
Chestnut-sided Warbler	Evergreen forest	No
Southern Central American highlands		
Philadelphia Vireo	Montane forest	Yes
Northern Andes, middle elevations		
Cerluean Warbler	Montane forest	No
Blackburnian Warbler	Montane forest	Yes
Canada Warbler	Montane forest	Yes
Scarlet Tanager	Montane forest	Yes

^aThe geographical boundaries that Terborgh uses to define neotropical migrant species differ from those used in table 2. Consequently, table 3 includes some additional species not listed in table 2.

Though Brash (1987) attributed an 11.6% avian extinction rate (from 1508 to 1980) in Puerto Rico to deforestation, the affected species were permanent island residents rather than neotropical migrants. In tropical deciduous forests of Puerto Rico, mist net samples dating back to 1972 revealed declines in numbers of wintering migrants (Faaborg and Arendt, in press). The near absence in recent years of formerly common Prairie Warblers and Northern Parulas and reductions in totals of other common species explained much of the decline in overall numbers. Because environmental conditions within and surrounding the Guanica Forest of Puerto Rico have apparently not changed, Faaborg and Arendt

suggested that severe variation in rainfall or island- or Caribbean-wide factors explained fluctuations in winter resident populations.

Two studies comparing populations of neotropical migrants wintering in large and small forest tracts yielded conflicting results. Robbins et al. (1987) found no differences in overall capture rates of migrants wintering in forest patches and extensive forest tracts of Costa Rica, Mexico, Puerto Rico, Jamaica, and the Dominican Republic. Only Gray-cheeked Thrush and Louisiana Waterthrush tended to be limited to large forest blocks. Askins et al. (in press) compared point surveys conducted in the extensive forests of St. John, U.S. Virgin

Islands, to those in the heavily fragmented forests of the nearby island, St. Thomas. Contrary to the findings of Robbins and his associates, migrants were significantly more common in the extensive forests of St. John than in the fragmented habitats of St. Thomas. But differences in study results could easily be related to differences in habitat types, migrant species, surrounding effects, and island/mainland factors.

By substituting space for time, the effects of deforestation can possibly be inferred from surveys of birds wintering in different successional stages. For instance, in a study conducted in the Mexican state of Campeche, Waide (1980) found that migrant assemblages shifted in species composition across a successional gradient from milpa (slash-and-burn fields) to secondary forests of different ages. Askins et al. (1990) inferred from Waide's results that local deforestation should ultimately favor some species while decreasing habitat for others. Rap-pole and Morton (1985) detected major declines in the populations of forest migrants after cutting of climax rainforest in southern Veracruz, Mexico. Even so, several migrant species maintained population levels after forest clearing, and others were able to subsist at reduced levels in the recently cleared area.

In comparisons of overwintering migrants using cleared and forested habitats, Greenberg (in press) found no consistent habitat differences in the degree of population decline over winter or in body condition. Despite large differences in density in forest and nonforest habitats, migrants appeared able to survive equally well on a per capita basis in either habitat. This led Greenberg to suggest that management of tropical second growth should effectively complement forest protection as an approach to conserving forest migrants.

Preservation of large blocks of mature tropical forest such as the Braulio Carillo National Park in Costa Rica are critical for maintaining biotic diversity and viable populations of migrant species (Stiles and Clark 1989). However, lands used for sustained-yield forestry or slash-and-burn agriculture with long fallow periods (>20 yr) should not be ignored as potentially useful habitats for protecting forest-dwelling migrants. If secondary tropical forests serve as important reservoirs of winter habitat for migrant species as argued by Lynch (1989), their sound management may very well prevent or reduce species extinctions (Lugo 1988). Economically feasible agricultural systems wherein woodlots, hedgerows, and shade canopies are maintained are additional alternatives that are worth encouraging on commercial lands (Askins et al. 1990).

Other Factors Having Potential to Cause Population Changes

Factors other than forest fragmentation in North America and deforestation in the Tropics are also responsible for population changes in neotropical migrants. Natural catastrophes such as hurricanes, flooding, rainfall, and drought can produce temporary local declines in population levels, effects that must be distinguished

from long-term regional declines. For example, patterns of annual variation for long-distance migrants breeding in northern Wisconsin and Upper Peninsula Michigan from 1985 to 1989 were highly correlated with drought indices (Blake et al., in press). During a 3-year period of moderate to extreme droughts, 8 of 11 long-distance migrant species in Wisconsin and 8 of 13 in Michigan declined in abundance. Knopf and Sedgwick (1987) detected population declines in selected migrant species in years following severe flooding of Colorado plains woodlands. Selected species that nested on or near the ground responded negatively to flooding, while species that nested above the ground showed no population changes. Responses in laying time, clutch size, and productivity to periodic flooding (Finch 1991a) may ultimately cause fluctuations in population size. Faaborg and Arendt (in press) concluded that rainfall patterns rather than habitat loss better explained population fluctuations of neotropical migrants wintering in Puerto Rico.

Populations of some bird species respond dramatically to extreme fluctuations in prey abundances. Several neotropical migrant species are known to specialize on spruce budworm and tent caterpillar outbreaks (e.g., Bay-breasted Warbler, Blackpoll Warbler, Tennessee Warbler, Cape May Warbler, Black-billed Cuckoo, Yellow-billed Cuckoo). Spruce budworm warbler populations rose and fell in clear association with high budworm densities in eastern Canada and New England from the mid-1960's and early 1970's and low budworm densities in the late 1970's and the 1980's (Robbins et al. 1986). The dispersed effects of tropical deforestation on migrant populations are likely to be concealed by such predator-prey dynamics on the breeding grounds.

Of potential threat to migrants overwintering in tropical habitats is the heavy use of fungicides, herbicides, and insecticides (Robbins et al., in press). Information is lacking to confirm whether exposure to pesticides deleteriously affects wintering populations of neotropical migrants. But, because pesticide use is greatest in commercial agricultural lands of large acreage, migrant species using such nonforest lands are probably at greater risk than forest specialists. Clearly, greater research effort is needed to assess habitat use, survivorship, and population trends of migrants occupying tropical non-forest lands treated with pesticides.

PROGRAM CONTRIBUTIONS BY FOREST SERVICE RESEARCH

RESEARCH CAPABILITY

The Research Branch of the USDA Forest Service (FS) has a strong nongame wildlife program with considerable emphasis on forest bird ecology, sensitive bird species, bird-habitat relationships, and avian responses to land use practices. Through sponsorship and publication of several timely symposia on nongame birds, the Forest Service has become a recognized leader in nongame bird research. With more nongame bird researchers than most other agencies and institutions, FS

Research is particularly well-suited to study neotropical migrants.

Twenty-one research work units (about 32 scientists) distributed among eight Experiment Stations have ongoing studies on nongame birds. Most units are distributed in favorable research locations to undertake new studies on neotropical migrants. The Forest Service can additionally support external research by providing funds through matching grants, cooperative agreements, and postdoctoral appointments. Because information on winter habitat requirements and population trends of nonbreeding migrants is notably lacking, new research cooperative efforts are especially needed in Latin American countries. Priority should be given to those research locations and habitats where gaps in knowledge are greatest or where threats to migrants are highest. For example, in North America, gaps in knowledge are greatest in the West and in the southeastern United States. While increased research efforts are recommended throughout Latin America, studies of migrant habitat requirements in different land use treatments are especially needed to facilitate management of viable populations on disturbed tropical lands.

Research that highlights migratory birds will complement other FS National Research Programs. Ongoing programs with tie-ins to research on neotropical migrants involve biological diversity; threatened, endangered, and sensitive species; forest health monitoring; and tropical forestry. In particular, FS research that focuses on tropical forest ecology, reforestation methodology, sustained-yield forestry, and resource economics will provide valuable information to Latin American countries. The wise use of tropical forests by indigenous cultures depends to a large extent on how well informed they are about forest management practices and resource conservation. FS Research can assist developing countries by contributing technical expertise, training programs, and educational materials on the management, use, and conservation of tropical forest resources.

CLARIFICATION OF RESEARCH NEEDS AND QUESTIONS

Below is a sampling of research needs, many of which vary geographically. Internal and cooperative studies by the Forest Service and other partners will be required to answer these and additional questions.

Analyses of Monitoring Data and Techniques

Many bird count methods produce biased abundance estimates and unreliable trend results. Research is needed to determine what procedures are accurate and appropriate for monitoring populations of migratory and resident birds in breeding and wintering areas. While the degree of bias connected with a particular technique or analytical approach often varies by species and habitat, methods that are suitable for a variety of situations need to be identified. To distinguish regional pat-

terns in population trends, it is imperative that trends can be compared. Thus, a standardized monitoring protocol must be applied.

One such method is the Breeding Bird Survey (BBS) operated by the U.S. Fish and Wildlife Service. Many scientists question the reliability of the Breeding Bird Survey because counts are conducted by volunteers, and because survey routes are limited to roads (roadside habitats may not be typical). Studies assessing the reliability of BBS data can help to pinpoint weaknesses in the method so that changes, improvements, or replacements can be made.

In addition, Forest Service Research has the capability to analyze and interpret existing survey data and assess the effectiveness and accuracy of other methods. Breeding Bird Survey routes have been established by the U.S. Fish and Wildlife Service since 1966, but much of the resulting data have not been analyzed. The Breeding Bird Census (BBC), which supplies estimates of bird densities in specific plots, is another data set that has not been sufficiently processed. Using BBS or BBC data, the population status of migrants breeding in isolated forest tracts or stands fragmented by differing land use treatments can be compared to population trends in intact forests. Similarly, BBS or BBC data can be compared among different managed habitats and land use activities, among National Forests and FS Regions, and among different land ownerships. Insufficient numbers of routes established in particular areas or habitats may limit certain comparisons.

Collaboration with the Fish and Wildlife Service is recommended for establishing new census routes and other bird population monitoring procedures on National Forest System (NFS) lands, to coordinate volunteers, and to structure data sets into formats suitable for Forest Service applications. The need for comparing bird trend data with habitat data produced from Forest Inventory Assessments (USDA Forest Service 1985) and other habitat monitoring programs (e.g., data generated by the Environmental Monitoring and Assessment Program planned by the U.S. Environmental Protection Agency (EPA), Hunsaker et al. 1990, U.S. EPA 1990) should also be addressed. If census data are grouped and analyzed based on NFS management boundaries, the resulting interpretations and recommendations will be suitably framed for immediate use by FS managers. Ideally, FS managers can incorporate results of survey analyses directly into habitat relationships models. FS managers will find bird status and trend information valuable for identifying sensitive species or groups of species on National Forest lands; for justifying and developing management strategies for migrants in Forest Plans; and for earmarking critical migrant habitats to restore, protect, or improve.

The Need for a Monitoring Network in Latin America

Few quantitative data are available on population trends of wintering migrants, and no regional monitor-

ing strategy is currently in place in the Neotropics. To assess long-term population responses to forest clearing and other land use activities in tropical regions, population monitoring networks and national data banks must be established. While North American agencies and cooperators can assist in the development of a monitoring network, the success of such a program depends on the internal coordination of Latin American and Caribbean agencies, technical experts, and volunteers. The Forest Service can provide training to interested participants in developing countries through the Tropical Forestry Program, but cooperative planning between Latin Americans and facilitating North American agencies like the U.S. Fish and Wildlife Service, the Smithsonian Institution, the Canadian Wildlife Service, and other organizations is essential.

Research is needed to evaluate the reliability of different bird count methods in tropical regions, to identify survey programs currently underway, and to determine the feasibility of implementing a region-wide monitoring system. Are the monitoring methods that are typically applied in Latin America (e.g., mist-netting, point counts) adequate to distinguish population changes over short and long periods of time and among different habitats, including different silvicultural treatments? What improvements or changes in methodology are recommended? The availability of Christmas Bird Count (CBC) data should be assessed to determine its usefulness in evaluating population trends of birds wintering in the Neotropics. Analyses of modern CBC data may offer some insights into patterns of population changes of wintering migrants (e.g., Norton, in press).

Resolution of Questions About Migrant Population Trends

Many controversial questions have yet to be resolved. In particular, region-wide declines in neotropical migrants have not been unequivocally confirmed. Further research is needed to verify the nature and extent of the problem and to understand the relative importance of observational scale, geographical boundaries, migratory status, and species habitat use. Lack of consensus in study results and interpretations impedes implementation of an international program to conserve neotropical migrant birds. Some general questions and research priorities are outlined below.

1. It is still not clear what factors are responsible for the population declines of migratory landbirds, or what species are at greatest global risk. Is the problem primarily on the breeding grounds, on the wintering grounds, or in both areas?
2. Six neotropical migrant species are federally listed as threatened or endangered in the United States: Peregrine Falcon, Bachman's Warbler (probably extinct), Kirtland's Warbler, Golden-cheeked Warbler, Black-capped Vireo, and Least Bell's Vireo (table 2). These species do not select similar habitats, nor are all habitats forested. Are these spe-

cies jeopardized by the same factors that are causing population declines in other migrant species? Are some unlisted species candidates for federal listing, or for designating as FS "sensitive species"? To support viable populations of migrant species that are not at risk of becoming threatened or endangered, what habitat characteristics should be maintained, and what population sizes and species distributions are needed?

3. Are the population declines widespread or local in scope? One approach to resolving this question is to compare long-term population trends between large, intact forests and small forest remnants. The same sets of species and habitats should be assessed in both small and large forests.
4. If population declines of neotropical migrants are associated with local factors like forest area and isolation, do cumulative local effects result in widespread population declines of forest-interior species? In other words, what is the net result of local extinctions and colonizations in a landscape or region? To balance colonization and extinction rates, it is necessary to summarize population trends at scales larger than a single forest patch.
5. Are the population declines limited specifically to neotropical forest-dwelling migrants? That is, are declines a function of migratory status and habitat use? Or is the problem larger (or smaller) or more variable in scope, such that classifications by migratory status, habitat, region, etc. mask the true nature of the problem?

What Are the Effects of Land Use Practices?

Ongoing forest management activities on private and federal lands present opportunities to assess migrant population responses to changing environmental conditions. To fully understand the problem of forest fragmentation, the relative roles of forest area and isolation, habitat structure and heterogeneity, species habitat use, and population responses should be defined in the context of land use practices. This information is needed on both breeding and wintering grounds.

1. Do the effects of forest fragmentation on populations differ among: species? geographical regions? habitat types? land use treatments or practices? landscapes with different habitat quantities? How are these differences expressed? Should the overall problem be redefined based on these differences?
2. Survival rates, habitat use, reproductive requirements, and viability of migrant populations in different silvicultural treatments are poorly understood. What land use and management activities contribute to declining, stable, or increasing populations?
3. Individual species have experienced population declines in some physiographic regions but not in

others. Are these declines associated with land management activities (e.g., clearcutting, fire suppression, livestock grazing, urban development) that vary by geography and habitat type? If so, then research and conservation efforts should target specific physiographic strata.

4. Are population declines of individual species in proportion to the amount of land converted, or do some species respond with disproportionate sensitivity to the amount of forest (or other habitat) lost?
5. What management designs and habitat improvements are necessary to maintain biological diversity and population viability on multiple use lands? Development of innovative landscape management methods, biodiversity models, or response guild models may be necessary, given that so many neotropical migrant species are involved. The field-testing and modification of available habitat relationships models (e.g., Robbins et al. 1989b, Temple and Cary 1988) are also highly recommended. Useful models should be capable of predicting how populations of single species or sets of sensitive species (e.g., forest-interior migrants) respond to changes in forest size, isolation distance, overall habitat quantities and mosaics, interspecific interactions, and land use treatments.

How Valuable Are Migration Corridors and Stopover Sites?

The availability of suitable habitat for migrating birds may influence survival and population stability of neotropical migrants (Hutto 1985). Successful migration depends on whether birds can replenish energy reserves rapidly; locate suitable stopover sites and travel routes; avoid predation in unfamiliar habitats; and cross travel barriers quickly and safely (Lindstrom 1989, Metcalfe and Furness 1984, Moore and Kerlinger 1987, Moore et al. 1990). The time available to search for superior habitats during migration may limit habitat choice (Ward 1987). Because of time and energy constraints, migrating birds may be particularly vulnerable to alterations and losses of in-transit habitats.

1. How do birds in migration respond to disturbance or disruption of migration corridors, staging grounds, stopover sites? Can birds adapt to loss of migration habitat, or do habitat losses result in impaired ability to return to breeding or wintering sites, ultimately causing population reductions? Identify critical habitat flyways or stopover sites that should be restored, improved, or protected.
2. What shapes, sizes, and orientations (east-west, north-south) of migration corridors and stopover sites determine habitat selection by migrating birds? What other factors influence or limit habitat use during migration? Develop methods for managing migration habitats.

3. Evaluate how behavior, survival, and population size vary in response to natural variation or experimental manipulations (e.g., "improvements") of migration habitat, and identify species that are highly sensitive to habitat alterations.

What Is the Status of Migrants in Western North America?

Research studies evaluating the population status and trends of neotropical migrants in western North America are critically needed. Region-wide data sets (e.g., BBS data) have not been adequately analyzed, and local data sets are either lacking or have not been summarized. Possible population declines reported in specific localities (e.g., Marshall 1988) should be investigated further. Western migrants may be experiencing problems similar to, or unlike, those of eastern birds (Love 1990).

The neotropical migrants that breed in the West reside primarily in riparian habitats and montane forests rather than in extensive western grasslands and shrub-steppe (Terborgh 1989). Because their habitats are restricted in distribution, total populations of western migrants may be much smaller than those of eastern species, making them particularly vulnerable to disturbance (Terborgh 1989). Factors that limit populations of eastern species may not apply to migrants that occupy western habitats of naturally small size (e.g., narrow riparian zones). Travel barriers like the Great Plains and the Rocky Mountains may limit dispersal ability, range expansion, and elevational habitat use of western migratory songbirds (Finch 1989, 1991b). A better understanding of migrant population responses and adaptations to unique features of riparian habitats (e.g., long and narrow shapes of riparian corridors; large amounts of natural edge; proximity to water; periodic flooding) is needed before on-the-ground conservation strategies can be implemented. Because bird-habitat relationships have been studied for many western species, it may be possible to reorganize existing data and results by using migratory strategy as a grouping variable.

Some conclusions may be drawn by conducting a thorough literature review (e.g., Love 1990).

1. Are migratory bird populations declining, increasing, or stable in the West? Are population changes linked to tropical deforestation on the wintering grounds and forest fragmentation on the breeding grounds as has been suggested for populations in the eastern and north-central United States, or does a different set of factors affect western migratory birds?
2. Are forest-dwelling long-distance migrants impacted in the West as they are in the East? Or are species associated with other habitats and movement patterns at risk? To focus conservation efforts, managers need to know which habitats contain the highest proportions of migrants and the most sensitive species, i.e., where should biodiversity conservation activities best be located; what

resource-management practices affect populations in positive and negative ways; what habitats, species, and groups of species are at greatest risk; and what management activities provide for viable populations?

3. Are birds that breed in western habitats of limited distribution (e.g., riparian habitats, deciduous woodlands) particularly vulnerable, as hypothesized by Terborgh (1989)?
4. Are western migrants area-sensitive, responding negatively to decreasing habitat patch size? What other factors limit populations? For example, if different orientations of riparian corridors affect the likelihood of habitat interception and occupancy by migrating birds (Gutzwiller and Anderson, in press), then population sizes may vary greatly from site to site.

What Demographic and Biotic Factors Limit Populations?

Several hypotheses have been proposed to explain the disappearance of forest-interior migrant species from small isolated forests, yet only a few of these have been tested. Ignorance of the causal mechanisms that regulate migratory populations limits our ability to provide and maintain suitable habitats for specific bird species or assemblages. Bird population levels vary in relation to rates of survival and nesting success, which in turn depend on the densities and composition of competitors and predators, and the availability of nest sites and food. With good reason, Martin (in press) implores researchers to address these critical factors that limit bird populations. Answers to the following questions will clarify the processes through which forest fragmentation affect vulnerable bird species.

1. Do interspecific interactions affect bird habitat use and abundance in fragmented forests? Which biotic interaction(s) have significant effects on bird populations: competition (for food, predator-free space, nest sites, microhabitats), brood parasitism, predation? Can and should these effects be managed, and if so, how (e.g., by manipulating quantities of habitats, parasites, predators)?
2. Why are nests in edge habitats more vulnerable to predation or parasitism? Is nest exposure or accessibility increased because of changes in nest-site habitat, in adjacent habitat, in parental ability, in predator or prey species composition, and/or in predator, parasite, or prey densities?
3. What fitness components are affected by forest fragmentation? Several aspects merit further attention: nesting success, number of broods, clutch size, growth rate, laying time, mating success, time and energy expenditures, adult and fledgling survival, and return and recruitment rates.
4. What resources are limiting to neotropical migrants in fragmented forests? What limitations lead to

reduced habitat use or population size? To competition? To reduced survival and productivity?

5. The availability of cavity nest sites often limits breeding populations of secondary cavity-nesting birds. Are breeding densities, productivities, and habitat partitioning of cavity-nesting neotropical migrants (table 2) affected by hole competition and interspecific nest interference (e.g., Finch 1990)? More importantly, do species interactions and corresponding population changes of migratory cavity-nesters vary in relation to forest area size, distance to edge, and degree of habitat fragmentation?

Basic and Applied Research in Latin America

Lack of basic information about the population status, habitat specificity, behavior, and geographical ranges of neotropical migrant birds on the tropical wintering grounds hinders assessments and interpretations of cause-and-effect relationships. Many of the same research needs identified for birds on the breeding grounds also apply to wintering migrants.

1. Which long-distance migrant species are jeopardized by tropical deforestation, and why are they vulnerable? To answer these questions, basic research on individual species is required to assess habitat specificity/plasticity, geographical ranges, movement patterns, overwintering behavior and demography (e.g., survival of age classes by habitat type), and responses to disturbances and land use activities.
2. What geographical areas and habitat types are most impacted by forest clearing? What quantities, successional stages, and features of forested habitats are needed to support healthy populations of wintering migrants?
3. Do migrants on the wintering grounds respond to forest fragmentation in a manner similar to those on the breeding grounds? Are the same species affected in both areas, or does species susceptibility shift because of seasonal changes in behavior and habitat use? Studies of population responses to patch size, isolation, plant species composition, habitat structure, and habitat heterogeneity of tropical forests are needed.
4. What underlying processes (e.g., increased predation, resource competition, food shortages, increased energy expenditure) associated with clearing of tropical forests contribute to population declines? Can effects be monitored over the non-breeding period by evaluating survival rates, body condition, behavior? Are problems that originate in tropical regions responsible for reductions in survival and productivity on the breeding grounds?
5. How valuable are mature and old-growth tropical forests to wintering migrants? Do secondary

habitats such as second-growth forests, inactive fields, and active croplands and pastures also have significant value? Are population levels sufficient indicators of habitat quality and habitat preferences, or is it important to assess other population attributes as well (e.g., survival rates, movement patterns)?

6. What management strategies can be implemented on public and community lands to conserve biotic diversity and migrant populations? Given that Latin Americans need to apply economically feasible methods for managing crops, livestock, etc., what habitat improvements are recommended for commercial and subsistence lands?
7. Do other land use practices in tropical areas contribute to the population declines of neotropical migrants? In particular, what are the effects of agricultural pesticides on wintering birds? What solutions can be implemented to protect migrants and other biota from toxics?

FOREST SERVICE RESEARCH OBJECTIVES

In summary, agencies and cooperators lack sufficient information on the population status and causes of population changes of neotropical migrants to effectively conserve their populations on the wintering and breeding grounds. Existing information also needs to be synthesized for use by resource managers. The major research goal of the Neotropical Migratory Bird Conservation Program, as defined in the 1990 Atlanta report, is to "generate, synthesize, and communicate the information necessary to identify and implement appropriate conservation and management measures for the maintenance of healthy population of neotropical migratory birds, including the recovery of declining species." The Forest Service is contributing to this effort by addressing multiple research objectives as outlined by participants at the Atlanta workshop and repeated here:

- Verify the nature and extent of reported population declines through analyses of existing and new information and through comparisons of population trends among small and large forests, geographical areas, land use activities, and migratory strategies. This information is especially needed in the West where data sets and analyses are fragmented and incomplete.
- Determine what habitat, biotic, and behavioral factors limit populations and distributions of migrants on the breeding and wintering grounds.
- Determine what migrant species and habitats are at risk due to forest fragmentation and tropical deforestation; identify the processes through which these species are impacted; and propose conservation solutions.
- Determine population trends, survival rates, habitat use, reproductive requirements, and viable popu-

lation levels of neotropical migrants in relation to different landscape patterns, silvicultural treatments, and other land use activities.

- Assess the habitat value of travel corridors and stopover sites to migrating birds, and identify the factors that interfere with migration, survival of birds in passage, and selection of stopover and destination habitats.
- Determine if standardized monitoring techniques like the Breeding Bird Survey are adequate to distinguish population changes of migrants over short and long periods of time and among different habitats; if not, implement new or modified methods.
- Evaluate the reliability of different methods for estimating bird abundance in tropical and temperate habitats, and develop new or modified methods to count migrants.
- Develop new guidelines and innovative habitat relationships models and landscape designs that Forest Service managers can use to sustain migrant habitats, populations, and bird communities in North America.
- Evaluate the social and economic impacts of management for neotropical migrants (e.g., public acceptance, economic costs, and alternative silviculture).
- Develop and transfer technology to tropical countries that will address the problem of deforestation, including forest restoration practices that are ecologically sound; forest conservation incentives in rural areas; and methods of sustainable resource use that provide for the maintenance of biological diversity. Assist in developing cooperative networks to facilitate this exchange.

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This report was prepared in support of the National Fish and Wildlife Foundation's Neotropical Migratory Bird Conservation Program and the USDA Forest Service's role in the program. Recent analyses of data on forest-dwelling species, many of which are neotropical migrants, show population declines in many North American areas. The literature review summarizes current information on population trends of neotropical migratory birds and the factors affecting migrant populations on the breeding and wintering grounds. Opportunities for research, monitoring, and conservation of these migrants on Forest Service lands are discussed.

Keywords: Neotropical migratory birds, bird conservation, habitat fragmentation, tropical deforestation, bird population monitoring, Latin America, Caribbean Basin



Rocky
Mountains



Southwest



Great
Plains

U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

The Rocky Mountain Station is one of eight regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.

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